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Age profile in nine *Mantella* poison frogs from Madagascar, as revealed by skeletochronological analyses

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Skeletochronology has been successfully used to age temperate amphibians, enabling comparisons of longevity and the age at sexual maturity. To date, however, there have been few similar studies conducted using this technique in tropical amphibians. Here we present data on age structure and age at maturity for nine species of Malagasy *Mantella* frogs: *M. baroni*, *M. bernhardi*, *M.* sp. aff. *expectata*, *M. cowani*, *M. crocea*, *M. laevigata*, *M. nigricans*, *M. pulchra* and *M. viridis*. The genus *Mantella* includes some of the most threatened frog species in Madagascar, and also some of the most requested species for the international pet trade. The lack of basic information on the life history of these species in the wild is hindering the development of sustainable collection models. We analysed museum specimens and bone samples of free living individuals collected during several surveys in western and eastern Madagascar. All investigated species showed a comparatively short longevity (0-4 LAGs) and sexual maturity was reached on the 1st or the 2nd year of life.

INTRODUCTION



The island of Madagascar is one of the most extraordinary amphibian hot-spots in the World: there are reliable estimated to be as many as 465 species, and many new taxa are being

described at a very rapid rate (ANDREONE et al., 2008; VIEITES et al., 2009). Even though major progress has been made in describing the diversity of the Malagasy amphibian fauna, much still remains to be understood about the ecology and life history traits of most species, and about the practical implications for conservation.

One of the best known frogs of Madagascar are those belonging to the genus *Mantella*, the Malagasy poison frogs. Currently, 16 species have been already described, and a few others still wait for a formal description (GLAW & VENCES, 2007). Their fame is due mainly to their bright aposematic colouration, their diurnal behaviour and the relative facility to keep them in captivity (at least for some species), that make them among the most sought after frogs for the international pet-trade (ANDREONE et al., 2006; GLAW & VENCES, 2007). So far, it is commonly accepted that many *Mantella* species are threatened because of a combination of narrow distribution, increasing deforestation and habitat degradation and intensive collection (ANDREONE et al., 2005*a*). The most recent conservation assessment (ANDREONE et al., 2008; ANONYMOUS, 2009) highlighted three species (*M. aurantiaca*, *M. cowani* and *M. milotympanum*) as "Critically Endangered", and four as "Endangered" (*M. bernhardi*, *M. crocea*, *M. expectata* and *M. viridis*).

Whether the pet-trade could be a primary cause of conservation concern and population/species decrease for amphibians is still matter of controversy and is worth of a more in-depth investigations in the future. The impact of collection from the wild on most *Mantella* species is still poorly understood and information on the breeding biology of species is badly needed. The whole genus *Mantella* is now listed on CITES II (ANDREONE et al., 2005*a*, 2006), and the trade is managed through a system of annual quotas (TESSA et al., 2009). In terms of commercial exploitation, a review carried by RABEMANANJARA et al. (2008*b*) reported a total of about 230,000 individuals exported from Madagascar between 1994 and 2003. Although this number is quite low when compared to around two million *Hymenochirus* and 1.6 million *Cynops orientalis* referred to the importation trade for the USA in 1998–2002 (SCHLAEPFER et al., 2005), it still represents a considerable portion of traded amphibians, capable of generating important economic benefits.

Seen all these aspects, it is our conviction that a special attention should be paid to gathering life history data for most *Mantella* species, in order to assess a better comprehension of the threats affecting the species. Population estimates, fecundity and age structure are among the most important factors to be taken into consideration, and could help in drawing the conservation profiles of the traded species.

Despite the commercial interest in the genus, there is little information on *Mantella* life history traits in the wild (VENCES et al., 1999). Scattered information on longevity of Malagasy frogs (especially mantellas and other traded species) are available from observations from captive individuals published in herpetoculturist papers and books (e.g., STANISZEWSKI, 2001), or as web-literature (CAREY & JUDGE, 2000). So far, the value in terms of conservation utilisation of these data is highly questionable. First of all because they are often reported in a non systematic way, then because the husbandry conditions are usually very different from what is the reality in nature. For this reason we do not consider these data as indicative of the real maximum longevity of a species.

A robust method used to assess longevity is skeletochronology (CASTANET, 1975). It has been widely used for individual age determination (ANDREONE et al., 2002, 2005*b*; GUARINO et

al., 1998, 2008; TESSA et al., 2007; KUMBAR & PANCHARATNA, 2001). Here we report skeletochronological data of nine *Mantella* species which significantly add to information already available (GUARINO et al., 2008), and verify the congruence between maximum longevity and age at sexual maturity.

MATERIAL AND METHODS

We analysed bone samples of the following *Mantella* species: *M. baroni* (15 males and 9 females; data from GUARINO et al., 2008); *M. bernhardi* (20 males and 12 females); *M.* sp. aff. *expectata* (9 males and 6 females); *M. cowani* (14 males and 12 females; data from GUARINO et al., 2008); *M. crocea* (13 males and 1 female); *M. laevigata* (5 males and 5 females); *M. nigricans* (5 males and 5 females); *M. pulchra* (13 males, 12 females); and *M. viridis* (20 males and 20 females). A complete list of the analysed specimens and their provenance is given in tab. 1 and in app. 1. The individuals from the Isalo population, attributed to *M. betsileo* by CROTTINI et al. (2008), are here considered as a still undescribed species, *M.* sp. aff. *expectata* "South", according to GLAW & VENCES (2007). The individuals attributed to *M. crocea* populations (according to GLAW & VENCES 2007) were considered as *M.* cf. *milotympanum* by BORA et al. (2008).

Frogs were sampled during the rainy season (October-March), when they are active and show breeding habits. They were localized by sight and by acoustic emissions of males. Once captured, they were sexed (males are usually smaller than females and often show femoral glands, or have differential chromatic characters; see JOVANOVIC et al., 2006), and measured for snout-vent length (SVL, at the nearest 0.1 mm). For one species, *M. bernhardi*, the study was partly conducted on phalanges taken from wild (non-captured) individuals and partly from preserved specimens. In such a case, the third toe of each captured individual was cut in the field, put in 90 % ethanol and then processed for skeletochronology and genetical analysis. After toe-clipping, the specimens were released at the site of capture or conserved as museum voucher specimens. For all the other species, the phalanx was taken directly from preserved voucher specimens, now part of the herpetological collections of Museo Regionale di Scienze Naturali, Torino, Italy (MRSN), and Parc Botanique et Zoologique de Tsimabazaza, Antananarivo, Madagascar (PBZT).

In *M. bernhardi*, we analysed separately individuals of two different populations which differed for habitat conditions: the first one from a rather intact rainforest site (Mangevo) within the Parc National de Ranomafana, and the second one from a heavily deforested site (Ambohimandrozo) next to the presumed species' type locality (RABEMANANJARA et al., 2005; VIEITES et al., 2006).

The skeletochronological method followed the protocol used for other Malagasy amphibians (GUARINO et al., 2008). Phalanges were decalcified in 3 % nitric acid for 1 hour, sectioned at 12 μm and stained in Ehrlich's haematoxylin for about 15 minutes. Finally, two researchers observed independently the sections and counted the LAGs, using a light microscope. In individuals sampled at the beginning of the rainy season (just after the latency period), the last LAG is positioned close (sometimes coincident) to the external edge of the

Table 1. – Data on provenance of samples of species of the genus *Mantella* analysed by skeletochronology.

Species	Sites	Coordinates	Altitude m a.s.l.	Habitat	Period of collection
Mantella baroni	Antoetra	20°50.10' S 47°19.95' E	~ 1400	Montane fragmented rainforest	I–II.2003
Mantella bernhardi	Ambohimandrozo	21°28.43' S 47°33.37' E	~ 600	Secondary altered rainforest	I-II.2004
Mantella bernhardi	Mangevo	21°23.25' S 47°27.38' E	~ 500	Rainforest	I-II.2004
Mantella cowani	Antoetra	20°50.10' S 47°19.95' E	~ 1400	Montane fragmented rainforest	I-II.2003
Mantella sp. aff. *expectata*	Isalo	22°37.38' S 45°21.52' E	~ 800	Savannah, dry forest	XI-XII.2004
Mantella crocea	Fierenana	18°34.36' S 48°26.38' E	~ 910	Rainforest	XII.2003
Mantella laevigata	Masoala	15°18.01' S 50°03.09' E	~ 615	Rainforest	XI-XII.1998-1999
Mantella nigricans	Masoala	15°18.01' S 50°03.09' E	~ 615	Rainforest	XI-XII.1998-1999
Mantella pulchra	Fierenana	18°34.36' S 48°26.38' E	~ 910	Rainforest	I.1999
Mantella viridis	Antongombato	12°23 03' S 49°13 27' E	~120	Secondary forests, dry forest	I.2005

bone section because the maximal growth season has not yet started. In such cases we considered the external border of the section as a LAG itself.

Then, in order to estimate age at sexual maturity, we followed the criterion of LAG rapprochement as proposed by Kleinenberg & Smirina (1969) and widely used by other authors (e.g., Francillon-Vieillot et al., 1990; Léclair et al., 2005; Tsiora & Kyriakoupolou-Sklavounou, 2002). Therefore, the first decreasing interval between LAGs, which is supposed to indicate the attainment of sexual maturity, was identified for each section.

All numerical data were analyzed by Student's *t*-test. A probability level of $P \leq 0.05$ was considered as significant. We compared the values (mean ± standard deviation) of SVL, maximum LAG number and number of LAGs at the sexual maturity for males and females whose samples were greater than five individuals.

Results

At a qualitative analysis the bone sections of all the studied species were similar and composed of two concentric layers, which corresponded to the endosteal (the innermost) and periosteal (the outermost) bone (Fig. 1). In the periosteal bone, we noticed contrasted haematoxynophilic lines that were considered as reliable LAGs. In some individuals, similar

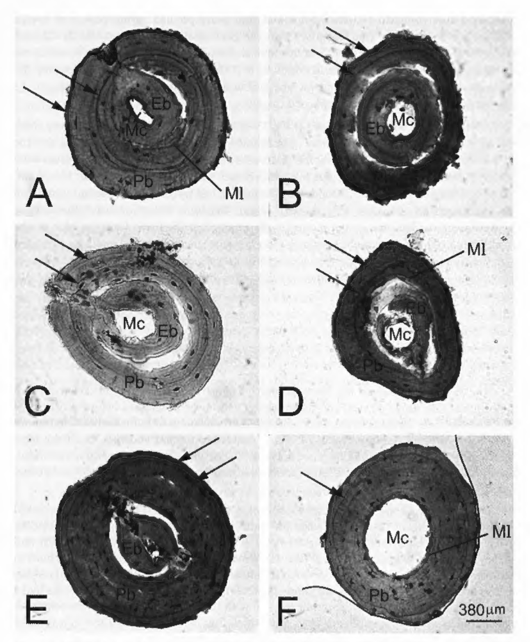


Fig. 1. – Histological section in the analysed *Mantella* species. Arrows indicate the lines of arrested growth (LAGs). A: *M. bernhardi*, MRSN A3112, female with 2 LAGs, SVL = 21.8 mm; B: *M.* sp. aff. *expectata*, MRSN A5234, male with 2 LAGs, SVL = 21.1 mm; C: *M. laevigata*, MRSN A4531, male with 2 LAGs, SVL = 24.8 mm; D: *M. pulchra*, MRSN A3060, female with 2 LAGs, SVL = 26.1 mm; E: *M. viridis*, MRSN A5082, female with 2 LAGs, SVL = 32.0 mm; F: *M. viridis*, MRSN A5112, male with 1 LAGs, SVL = 25.1 mm. Abbreviations: Eb, endosteal bone; Mc, medullar cavity; Ml, metamorphosis line; Pb, periosteal bone.

lines were also visible in endosteal bone and thus corresponded to the periosteal LAGs. Although a reversal line (the boundary between periosteal and endosteal bone) was not always easy to detect, we assumed that the bone erosion did not delete any LAGs, assuming the short longevity of these frogs. In addition, in 47.5 % of the specimens we detected the presence of the metamorphosis line, a line visible near the reversal line occurring at the passage from tadpoles to metamorphosed froglets.

All the species were small bodied (SVL 13-33 mm) and showed a comparatively short life span (0-4 LAGs). Females were significantly larger than males, excepting for the *M. bernhardi* population from Ambohimandrozo. In six species the mean LAG values were higher in females than in males, but these differences were significant only for *M. cowani*. Males and females reached sexual maturity the first or, less frequently, the second year, in all the species (mean ± SD = 1.37 ± 0.31 years). The only exception was observed for *M. laevigata*, in which the sexual maturity was attained at the second year in nine of the 10 individuals; in this species the longevity was two years, and thus sexual maturity coincided with the life expectancy. In all the species except for *M. pulchra*, males reached sexual maturity earlier than females, but the only species in which this difference was significant were *M.* aff. *expectata* and *M. viridis*.

Discussion

The data here presented represent the most exhaustive contribution on skeletochronology applied to a single tropical amphibian genus. Moreover, as stressed before, most of the analysed *Mantella* specimens came from series held in collections of natural history museums. So far, we advocate the importance of using preserved museum vouchers as a long-term source of biological data, and this is not only useful, but also relevant in conservation terms, since it maximises the amount of information that can be obtained from zoological collections (Tessa et al., 2009).

Our data also confirm that skeletochronology is reliable and successful for tropical amphibians, despite of their provenience and ecology. All the studied species showed evident LAGs, thus indicating that they observed a period of growth and a period of inactivity and latency, as this was witnessed by the differential bone deposition and different chromophily in bone sections. Although we cannot provide definitive conclusions about the life history of the species because of the small sampled numbers, we noticed that all of the analysed frogs had a short life span, and this could be put in relation with their small body size. Skeletochronological studies on anurans utilizing both sexes show that in most species there is a positive correlation between body size and age both in males and females (Ryser, 1988; Esteban et al., 1996, 1999). Moreover, there is often a wide size overlap among age classes even if body length and age are positively correlated.

Our results for nine *Mantella* species are consistent with longevity patterns observed in other amphibians of Madagascar, such as *Boehmantis microtympanum* (Guarino et al., 1998), *Dyscophus antongilii* (Tessa et al., 2007) and *Boophis tsilomaro* (Andreone et al., 2002). These species are much larger than mantellas, all exceeding 80 mm (with a body size

record in *D. antongilii* of 110 mm), and reach a maximum age of 11 years (in *B. microtympanum* and *B. tsilomaro*). In the *Mantella* species, the body miniaturisation, which is associated to mirmecophagy, diurnal activity, and poison segregation at skin level (see VENCES et al., 1998), is a limit for their maximum life expectancy that does not exceed four years in the wild.

In six species, males had a shorter longevity than females, but this difference was significant only for *M. cowani*. This population comes from a high plateau site at around 1400 m a.s.l. (GUARINO et al., 2008) In particular, males of this species showed short mean longevity, with 1.2 ± 0.2 LAGs, while females had 2.2 ± 0.2 LAGs. So far, we assume that females can effectively live more than males, and reach a larger body size, as shown in tab. 2. We do not have sound explanations for such a difference, but we may hypothesise that females carry out a much more hidden life, and thus are less subject to predation, this leading to a differential mortality between the sexes.

We also presented information about the age at sexual maturity from skeletochronology. This was reached quite early (< 1–2 years) in all the examined species, except for *M. laevigata*. This arboreal species (GLAW & VENCES, 2007) showed a different age profile, with sexual maturity reached at two years in all the examined individuals. Unfortunately, our sample was too small to draw such a significant explanatory hypothesis, but, probably, in this species the majority of the individuals reproduce after two years of age and possibly die just after. Most likely, the delay in reaching sexual maturity could allow to get a larger size that can be useful in males for the male-male fights over defended resources necessary for reproductive success and in females for maternal care (HEYING, 2001). More studies are needed on this species to understand whether this difference is constant and which could actually be the advantages for both sexes.

In general, males reach sexual maturity earlier than or at the same age as females, but the only significant differences were found in *M.* sp. aff. *expectata* (1.2 ± 0.1 versus 1.3 ± 0.2 LAGs) and in *M. viridis* (1.0 ± 0.0 versus 1.1 ± 0.1 LAGs). Notably, these are the only two species from open grassland habitats, with accentuated seasonality (TESSA et al., 2009).

In several anuran species, the sexes reach sexual maturity at the same age (ESTEBAN et al., 2004), whereas in others females reach sexual maturity later than males (CHERRY & FRANCILLON, 1992). These data may be explained by the fact that females start breeding when they reach a minimum body size to maximize clutch mass (CHERRY & FRANCILLON, 1992; ESTEBAN et al., 1996). On the other hand, in anuran females delayed maturity often means a larger body size and higher fecundity (GIBBONS & MCCARTHY, 1984), and sexual selection for larger body size in females occurs when it represents an important determinant of female reproductive success.

The age profile can also provide information on the conservation status of the studied species, as witnessed by the two studied *M. bernhardi* populations, which showed a different LAG number profile. The individuals from Mangevo, which is a rather intact rainforest, showed a comparatively larger body size and a longer life than those from the increasingly deforested site of Ambohimandrozo (SVL: males: $t = 1.88$, $P < 0.05$; females: $t = 4.44$, $P < 0.05$; LAGs: males: $t = 1.05$, $P < 0.05$; females: $t = 2.03$, $P > 0.05$). Instability of habitat quality and the intense degradation following anthropogenic may be invoked as a cause to decrease population viability.

Table 2. – Data on body size (SVL in mm), longevity (LAG numbers) and age at sexual maturity (given as LAG numbers, largely corresponding to years) in the analysed species. Values are provided as mean ± standard deviation. The numbers between round brackets refer to the number of analysed specimens, whereas the values between square brackets are the extreme range values; *t*, Student's *t* value; asterisked values are significantly different for $P < 0.05$ (*) or for $P < 0.01$ (**).

Species	Sex	SVL	*t*	Maximum number of LAGs	*t*	LAGs at sexual maturity	*t*
Mantella baroni	Males (15)	25.6 ± 2.4 [18.6-28.5]	3.48**	1.6 ± 0.2 [1-3]	1.07	1. ± 0.5 [1-2]	0.09
	Females (9)	28.6 ± 1.2 [26.9-30.1]		1.9 ± 0.1 [1-2]		1.4 ± 0.5 [1-2]	
Mantella bernhardi (Mangevo)	Males (10)	20.1 ± 0.8 [19.1-21.8]	-	1.8 ± 0.6 [1-3]	-	1.3 ± 0.5 [1-2]	-
	Females (2)	23.2 ± 0.7 [22.6-23.8]		2.5 ± 0.7 [2-3]		2.0 ± 0.0 [2]	
Mantella bernhardi (Ambohimandrozo)	Males (10)	19.3 ± 1.1 [17.1-20.5]	1.41	1.2 ± 0.8 [1-3]	0.98	1.0 ± 0.0 [1]	0.17
	Females (10)	20.0 ± 1.2 [18.1-21.8]		1.5 ± 0.9 [1-3]		1.1 ± 0.3 [1-2]	
Mantella cowani	Males (14)	25.7 ± 1.7 [15.1-28.9]	6.29**	1.3 ± 0.2 [1-2]	7.86**	1.0 ± 0.4 [1-2]	2.01
	Females (12)	29.3 ± 1.1 [27.9-31.4]		2.2 ± 0.2 [1-3]		1.3 ± 0.3 [1-2]	
Mantella crocea	Males (13)	17.2 ± 1.1 [14.8-19.5]	-	2.8 ± 0.7 [2-4]	-	1.2 ± 0.1 [1-2]	-
	Female (1)	21.6 -		2 [2]		2.0 [2]	
Mantella sp. aff. *expectata*	Males (9)	20.9 ± 1.5 [18.7-23.3]	4.53**	1.9 ± 0.8 [1-3]	0.26	1.2 ± 0.1 [1-2]	2.36*
	Females (6)	24.0± 1.0 [23.0-25.3]		1.8 ± 0.5 [1-2]		1.3 ± 0.2 [1-2]	
Mantella laevigata	Males (5)	24.2 ± 0.5 [23.7-24.8]	4.01**	2.0 ± 0.0 [2]	0.99	2.0 ± 0.0 [2]	0.00
	Females (5)	26.2 ± 1.0 [24.6-27.0]		1.8 ± 0.5 [1-2]		2.0 ± 0.0 [2]	
Mantella nigricans	Males (5)	25.1 ± 0.9 [24.1-26.0]	4.06**	2.8 ± 0.8 [2-4]	1.13	1.2 ± 0.1 [1-2]	0.00
	Females (5)	27.2 ± 0.7 [26.5-28.3]		1.8 ± 0.8 [1-3]		1.2 ± 0.1 [1-2]	
Mantella pulchra	Males (13)	20.6 ± 2.1 [18.4-22.7]	3.63**	1.9 ± 0.7 [1-3]	0.73	1.6± 0.1 [1-2]	1.07
	Females (12)	23.6 ± 2.0 [21.3-28.2]		2.1 ± 0.9 [1-4]		1.5 ± 0.2 [1-2]	
Mantella viridis	Males (20)	25.9 ± 2.1 [23.1-31.2]	8.42**	1.3 ± 0.6 [1-3]	1.43	1.0 ± 0.0 [1]	4.97**
	Females (20)	30.4 ± 1.2 [28.5-32.5]		1.6 ± 0.7 [1-3]		1.1 ± 0.1 [1-2]	

Our final consideration goes to the advantage of putting together a series of integrative data for conservation purposes. In particular, for the genus *Mantella*, the data on age structure, longevity and age at sexual maturity here presented represent a crucial complement to those on fecundity, distribution and population consistency (e.g., Rabemamanjara et al., 2008*a*; Tessa et al., 2009). All these parameters could be usefully utilised to test extinction probability of species and populations associated to the different threat causes using population viability analyses. In particular, by comparing the survival probability of threatened

species in relation to different pet-trade collection pressures may provide indications about the sampling limit for national and international trade. On the occasion of future works, longevity data should be integrated with data on the type and the state of the habitat, and the fragmentation and the density of each harvested population, so to implement tailored conservation programs.

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APPENDIX 1

LIST OF *MANTELLA* SPECIMENS USED FOR SKELETOCHROLOGICAL ANALYSIS

Abbreviations: MRSN, specimens housed in the Museo Regionale di Scienze Naturali, Torino; PBZT, specimens housed in the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo; Prov., Province; AA, surroundings of Antongombato and Montagne des Français; IM, Isalo Massif; MP, Masoala Peninsula.

Mantella bernhardi Vences, Glaw, Peyrieras, Bohme & Busse, 1994. – 7 unnumbered phalanges collected from wild individuals (Mangevo, Fianarantsoa Prov., 8.II.2004); MRSN A3112-3116 (Mangevo, Fianarantsoa Prov., 8.II.2004); MRSN A3042, 12 phalanges, PBZT (two unlabelled specimens, Ambohimandrozo, Fianarantsoa Prov., 15.II.2004).

Mantella sp. aff. *expectata* Busse & Böhme, 1992. – MRSN A5232-5233, A5325 (Antoha, IM, Fianarantsoa Prov., 3.XII.2004), MRSN A5223, A5225, A5228-5229, A5231, A5234-5236, A5238 (Tsitorina, IM, Fianarantsoa Prov., 3.XII.2004); MRSN A5237, A5239 (Kazofoty, IM, Fianarantsoa Prov., 2.XII.2004); MRSN A5230 (Sakavato, IM, Fianarantsoa Prov., 6.XII.2004).

Mantella crocea Pintak & Böhme, 1990. – PBZT unlabelled, likely Fierenana, Toamasina Prov.

Mantella laevigata Methuen & Hewitt, 1913. – MRSN A4475 (Antsarahan'Ambararato, MP, Antsiranana Prov., 4.XII.1999), MRSN A4533, A3000 (Andasin'i Governera, MP, Antsiranana Prov., 6.XII.1998), MRSN A4531-4532 (Andasin'i Governera, MP, Antsiranana Prov., 7.XII.1998); MRSN A3001-3002 (Andasin'i Governera, MP, Antsiranana Prov., 9.XII.1998), MRSN A2999 (Behanjada, MP, Antsiranana Prov., 22.XI.1999); MRSN A4505-4506 (Menamalona, MP, Antsiranana Prov., 11.XII.1999).

Mantella nigricans Guibé, 1978. – MRSN A4457 (Andasin'i Governera, MP, Antsiranana Prov., 5.XII.1998), MRSN A4467 (Ambatoledama, MP, Antsiranana Prov., 17.XI.1998); MRSN A4454 (Ambatoledama, MP, Antsiranana Prov., 16.XI.1998); MRSN A4508 (Antsarahan'Ambararato, MP,

Antsıranana Prov, 30.IX 1999), MRSN A4472 (Antsarahan'Ambararato, MP, Antsıranana Prov, 29 XI.1999), MRSN A4456 (Behanjada, MP, Antsıranana Prov., 17.XI.1998); MRSN A4480 (Menamalona, MP, Antsıranana Prov, 11 XII.1999), MRSN A4481 (Menamalona, MP, Antsıranana Prov, 15 XII 1999), MRSN A4482 (Menamalona, MP, Antsıranana Prov, 11.XII.1999); MRSN A4503 (Menamalona, MP, Antsıranana Prov., 15.XII 1999)

Mantella pulchra Parker, 1925. PBZT unlabelled, Fıerenana, Toamasına Prov.; MRSN A3060-3062 (Corrıdor bethween Moramanga and Zahamena, Tamatave Prov., 10 I.1999); MRSN A2753, 2754 (An'Ala, Tamatave Prov, 1 III 2003), MRSN A59(2-4) (An'Ala, Tamatave Prov, 4.I 1992), MRSN A4487, A4489 (Andasıbe surroundıngs, Tamatave Prov., 1.I.1995).

Mantella vırıdıs Pıntak & Böhme, 1988. – MRSN A5055, A5073, A5077 (Ambovomany, AA, Antsıranana Prov, 15 I 2005), MRSN A5102, A5112 (Ambodımanga, AA, Antsıranana Prov., 17.I 2005), MRSN A5064, A5070, A5076, A5094 (Andamanga, AA, Antsıranana Prov., 4.I.2005); MRSN A5075, A5080-5081, A5095, A5097, A5106 (Andronotsımety Ambıney River, AA, Antsiranana Prov., 8 I 2005), MRSN A5095, A5117 (Andohenimangoko, AA, Antsiranana Prov., 15.I 2005); MRSN A5056 (Anketrabe, AA, Antsıranana Prov., 6.I 2005), MRSN A5066 (Anosıravo, AA, Antsıranana Prov., 24 I.2005), MRSN A5088 (Antonboko, AA, Antsıranana Prov, 6 I.2005); MRSN A5054, A5096 (Anjanaharıbe, AA, Antsıranana Prov., 8 I.2005); MRSN A5050, A5052, A5067 (Antonboko, AA, Antsıranana Prov., 21 I.2005), MRSN A5115 (La Mere Rouge, AA, Antsıranana Prov., 7.I 2005); MRSN A5113-5114, A5124, A5127 (Maleja, AA, Antsıranana Prov, 7 I 2005); MRSN A5063, A5121 (Mahatsınjo, AA, Antsıranana Prov., 17.I.2005), MRSN A5107 (Porchuıte, AA, Antsıranana Prov., 8 I.2005); MRSN A5060 (Tsımanankaratre, AA, Antsıranana Prov, 8 I 2005), MRSN A5082 (Tegnan Antshampano, AA, Antsıranana Prov, 8.I.2005), MRSN A5100 (Tsımanankaratre, AA, Antsıranana Prov., 8.I.2005)

Tadpole morphology and table of developmental stages of *Polypedates teraiensis* (Dubois, 1987)

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Breeding specimens of *Polypedates teraiensis* are commonly seen during monsoon among vegetation near lentic water bodies in Assam, northeastern India. Early life history stages, the normal development, is described and illustrated based on GOSNER's (1960) 46 developmental stages. The morphology and the buccal features of a stage 38 tadpole are described in detail and illustrated. At ambient temperature (26°C to 32°C), completion of the entire development from ovum fertilization up to emergence of the froglet took 58 days (1392 hours). A comparison with larvae of congeneric species is provided, including a discussion on the advantages of their embryonic development in a foam nest.

INTRODUCTION

Polypedates leucomystax (Gravenhorst, 1829) has long been thought to be a very widely distributed species. Modern methods, such as bioacoustics and molecular techniques, allowed recognizing cryptic species (e.g., MATSUI et al., 1986, NARINS et al., 1998). Taxonomic revisions of this species complex remain to be done in various parts of its range. They will likely result in description of new species (BROWN et al , 2010). This complex has not been well-studied in northeastern India where at least six species are currently recognized: *Polypedates assamensis* Mathew & Sen, 2009; *Polypedates maculatus* (Gray, 1830); *Polypedates megacephalus* Hallowell, 1861; *Polypedates subansiriensis* Mathew & Sen, 2009; *Polypedates taeniatus* (Boulenger, 1906); and *Polypedates teraiensis* (Dubois, 1987) The status of *Polypedates maculatus himalayensis* (Annandale, 1912), which is either considered as a synonym of *P. maculatus*, *P. leucomystax* or *P. teraiensis* (FROST, 2010 [http://research.amnh.org/vz/

herpetology/amphibia/; accessed on 24th April 2010]), a subspecies of *P. maculatus* (Annandale, 1912; Dubois, 1987), or a valid species (Ahmed et al., 2009, Mathew & Sen, 2009) remains to be solved. Adults of *P. teraiensis* are morphologically closer to *Polypedates mutus* (Smith, 1940) than to *P. leucomystax* (Dubois & Ohler, pers. comm.). Adults of *P. teraiensis* and *P. mutus* are large, have co-ossified skulls, have always longitudinal stripes on their backs, and large spots on back of thighs. However, *P. teraiensis* has vocal sacs whereas they are absent in *P. mutus* (Dubois, 1987; Dubois & Ohler, pers. comm.). Additional characters of adult morphology are particularly needed to understand this difficult group. Tadpole morphology and development is one of the most important life history traits that could add important information to our knowledge of this genus. Among the species of *Polypedates* occurring in northeastern India, only the larvae of *P. maculatus* and *P. megacephalus* have been previously described (Mohanty-Hejmadi & Dutta, 1988; Chou & Lin, 1997).

Normal tables of development are very useful for studies of comparative development as well as for a variety of experimental and descriptive studies on any species. Normal developmental tables are available for the following Indians anurans: (1) Dicroglossidae. *Hoplobatrachus tigerinus* (Daudin, 1802) (Khan, 1969, Agarwal & Niazi, 1977), *Fejervarya "limnocharis* (Gravenhorst, 1829)" (Roy & Khare, 1978) and *Euphlyctis cyanophlyctis* (Schneider, 1799) (Kumar, 1982); (2) Hylidae *Hyla annectans* (Jerdon, 1870) (Ao & Bordoloi, 2001). Partial developmental tables are available for the following Indian Rhacophoridae: *P. "leucomystax"* (Kiyasetuo & Khare, 1986), *P. maculatus* (McCann, 1932, Mohanty-Hejmadi & Dutta, 1988) and *Rhacophorus malabaricus* Jerdon, 1870 (Sekar, 1990). Some developmental data were provided for the dicroglossid *Sphaerotheca breviceps* (Schneider, 1799) and the microhylid *Uperodon systoma* (Schneider, 1799) (Mohanty-Hejmadi et al., 1979*a-b*).

Herein, we describe and illustrate the embryological and larval development of *Polypedates teraiensis* throughout the 46 stages of Gosner's (1960) standard table. Furthermore we describe the morphology and buccal anatomy of a stage 38 tadpole. Completion of the whole development from ova fertilization to froglets took 58 days (1392 hours) at a room temperature ranging from 26°C to 32°C.

Material and methods

Amplecting adults of *Polypedates teraiensis* were collected at various dates between 2nd February 2002 and 17th August 2006 at different sites of Guwahati city (Assam state, northeastern India). Amplecting pairs were subsequently transferred to glass aquaria (60 × 45 × 45 cm, with 20 cm of water and sloping sand on one side) where they laid eggs in a foam nest within 12 hours. Our data are based on five clutches, laid by five different pairs, that were kept until the end of metamorphosis. The eggs were reared under laboratory conditions and the entire development was recorded. Each clutch was reared in a separate aquarium, the number of individuals decreasing subsequently as larval samples were taken and fixed for description of the developmental process and as voucher for the developmental table. Tadpoles were fed plankton and algae (mostly *Spirogyra* ssp.) from natural habitat. Specimens were preserved in 8 % formaldehyde solution and stored in the herpetological collection at the Museum of the

Institute of Advanced Study in Science and Technology of Guwahati, under collection numbers IASST.AT 731 IASST AT.1170. Staging follows GOSNER (1960). Sampling was repeated for three successive years and the average data are presented herein. Only stages 16 and 19 were not collected. Morphological terminology follows ALTIG & MCDIARMID (1999) and Keratodont Row Formula (KRF) follows DUBOIS (1995). Measurements were taken on preserved specimens. The stage 38 tadpole description is provided separately. The measurements, done with the help of a dial vernier calliper, are given to the nearest 0.1 mm. Morphological landmarks follow ALTIG & MCDIARMID (1999 26, fig 3 1) and GROSJEAN (2006) except for FLL, HH, HL, HLL, SE, SpE and SpN Study of the buccopharyngeal anatomy was done with a Scanning Electron Microscope (SEM) model No. JSM-6360 at the North Eastern Hill University (NEHU), Shillong (India). The terminology of buccal structures follows WASSERSUG (1976).

ABBREVIATIONS

BH, maximum body height, BW, maximum body width; ED, maximum eye diameter; FLL, forelimb length; HH, maximum head height; HL, head length (from tip of snout to posterior margin of eye), HLL, hind-limb length (from insertion of limb to tip of 4th toe); IOD, interorbital distance (distance between the centres of the pupils); KRF, keratodont row formula; MTH, maximum tail height; NP, nare-pupil distance (from centre of nare to centre of pupil); NN, internarial distance; ODW, oral disc width; SE, snout-eye distance (from tip of snout to anterior edge of eye); SN, snout-nare distance; SpE, spiracle-eye distance (from opening of spiracle to centre of pupil); SpN, spiracle-nare distance (from opening of spiracle to centre of nare); SSp, distance from tip of snout to opening of spiracle; SVL, snout-vent length; TAL, tail length; TL, total length

RESULTS

NATURAL HISTORY AND PHYSICO-CHEMICAL ANALYSIS OF TADPOLE HABITAT

Polypedates teraiensis begins to breed early in the year. It breeds sporadically after the first few rains of the rainy season, usually in the month of March. Normally, the frogs produce foam nests that are attached to vegetation above shallow temporary waters. However, foam nests have been observed on logs or walls of human habitations far from water; these foam nests were desiccated or decayed. Foam nests or tadpoles were never found in running water. The following physico-chemical characteristics were noted In the present study the value of dissolved oxygen was between 3 3 and 7.4 mg/l and that of free CO_2 was between 1.7 and 6 2 mg/l; total alkalinity was between 51 and 84 mg/l and total hardness was between 20 and 59 mg/l The values of dissolved oxygen and free carbon dioxide are highly variable as they are greatly influenced by the decomposition process.

Developmental table

The clutch size of the five nests was 67, 114, 127, 120 and 75 eggs ($x = 100.6 \pm 27.6$). The eggs were uniformly white in colour Eggs on the outermost surface of the foam nest sometimes did not develop and turned pale yellow due to desiccation.

Stages 1 to 19 were completed within the foam nest. The embryos hatch at stage 20 and stay within the nest until stage 22 when they drop down in water to complete metamorphosis. The characteristics of each stage are presented below.

1. Gosner Stage 1 (fig. 1)

Age. 0 h.
Diameter. – 2.0–2.2 mm.
Characters. – Fertilized egg, spherical in shape. Egg uniformly white in colour

2. Gosner Stage 2

Age. – 0 h 50.
Diameter. – 2.0–2.2 mm.
Characters. – One cell stage, just before the start of cleavage.

3. Gosner Stage 3 (fig. 2)

Age. – 2 h 25.
Diameter. – 2.0–2.2 mm
Characters. Two cells stage. Start of cleavage: the meridian cleavage furrow originates at the animal pole and proceeds to the vegetal pole, dividing the egg completely into two equal blastomeres.

4. Gosner Stage 4 (fig. 3)

Age. – 3 h 10.
Diameter. – 2.0–2.2 mm.
Characters. Four cells stage The second meridian furrow, which starts at the animal pole, extends to the vegetal pole at a right angle to the first.

5. Gosner Stage 5 (fig. 4)

Age. – 3 h 55.
Diameter. – 2.0–2.2 mm.
Characters. Eight cells stage. The third cleavage is horizontal, slightly above the equator, forming eight blastomeres, four smaller micromeres in the animal pole and four bigger macromeres in the vegetal pole.

6. Gosner Stage 6 (fig. 5)

Age. 4 h 35.
Diameter. – 2.0–2.2 mm.
Characters. – 16 cells stage. The cleavage furrow is vertical. First the micromeres are divided into eight cells, resulting in twelve cells in total (eight micromeres and four

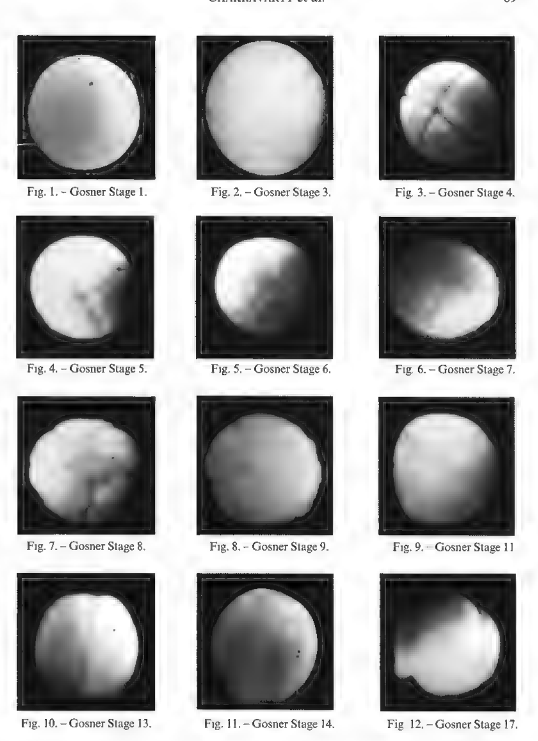


Fig. 1. – Gosner Stage 1.

Fig. 2. – Gosner Stage 3.

Fig. 3. – Gosner Stage 4.

Fig. 4. – Gosner Stage 5.

Fig. 5. – Gosner Stage 6.

Fig. 6. – Gosner Stage 7.

Fig. 7. – Gosner Stage 8.

Fig. 8. – Gosner Stage 9.

Fig. 9. – Gosner Stage 11

Fig. 10. – Gosner Stage 13.

Fig. 11. – Gosner Stage 14.

Fig. 12. – Gosner Stage 17.

Fig. 1 to 12 Developmental stages 1 17 (GOSNER, 1960) of the embryo of *Polypedates teraiensis*.

macromeres) This is followed by the division of the four macromeres as the cleavage furrow reaches the vegetal pole, resulting in 16 cells.

7. Gosner Stage 7 (fig. 6)

Age. – 5 h 35.

Diameter. – 2.0–2.2 mm

Characters. – 32 cells stage. The latitudinal cleavage furrows of the micromeres and macromeres result in the formation of 16 micromeres and 16 macromeres.

8. Gosner Stage 8 (fig. 7)

Age. – 8 h.

Diameter. – 2.0–2.2 mm.

Characters. – Morula stage. Cell proliferation increases the embryo to more than 64 small blastomeres. The surface of the animal pole resembles a cluster of beads.

9. Gosner Stage 9 (fig. 8)

Age. – 9 h 56.

Diameter – 2 0–2 2 mm

Characters. Blastula stage. The blastomeres are minute in size and the surface of the egg appears granular.

10. Gosner Stage 10

Age. – 16 h.

Diameter - 2 0–2 2 mm

Characters. Early gastrula stage. The dorsal lip of the blastopore has formed and is crescent-shaped. The zone of the vegetal hemisphere is reduced due to migration (epiboly) of the micromeres towards the vegetal pole.

11. Gosner Stage 11 (fig. 9)

Age. – 19 h.

Diameter. – 2 0–2.2 mm

Characters. Mid-gastrula stage. The epibolic migration of micromeres over the vegetal pole reduces the exposed area of macromeres, which is surrounded by the lateral lips of the semicircular or horse shoe shaped blastopore.

12. Gosner Stage 12

Age. – 21 h.

Total length. – 2.0–2.3 mm.

Characters. – Late gastrula stage. The blastopore, initially ventral, becomes the posterior pole of the antero-posterior axis.

13. Gosner Stage 13 (fig. 10)

Age. – 24 h.

Total length. – 2.0–2.3 mm.

Characters. – The embryo is slightly elongated. A ridge is observed on one side. The protruding plug of yolk cells gradually disappears and the neural plate develops as a tubular area along the dorsal surface.

14. Gosner Stage 14 (fig. 11)

Age. – 36 h.

Total length. – 2.0–2.4 mm.

Characters. – Embryo elongate, slightly oval. Neural fold present: elevation of two lateral ridges separated by the neural groove.

15. Gosner Stage 15

Age. – 56 h.

Total length. – 2.0–2.6 mm.

Characters. – Embryo oval in shape. Period of active ciliary rotation, during which the neural groove narrows and the folds approach each other.

16. Gosner Stage 17 (fig. 12)

Age. – 62 h.

Total length. – 2.2–2.8 mm.

Characters. – Appearance of tail bud at the posterior tip of the embryo which is wider than long.

17. Gosner Stage 18 (fig. 13)

Age. – 71 h.

Total length. – 2.9–3.1 mm.

Characters. – Head region well defined with optic and gill plates bulges. Body elongated, tail bud elongate and rolled up around the body. This stage is recognized by the initiation of muscle contraction.

18. Gosner Stage 20 (fig. 14)

Age. – 104 h.

Total length. – 4.7–5.3 mm.

Characters. – The embryos hatch but the larvae remain within the nest. Large yolk reserve. Tail prominent, slightly curved ventrally. Gills distinct.

19. Gosner Stage 21 (fig. 15)

Age. – 118 h.

Total length. – 6.8–7.7 mm.

Characters. – Tail fins opaque. The yolk reserve is quite large and elongated. Eyes distinct, cornea transparent. Gills developing. Very light pigmentation on the dorsal side but not around the eyes.

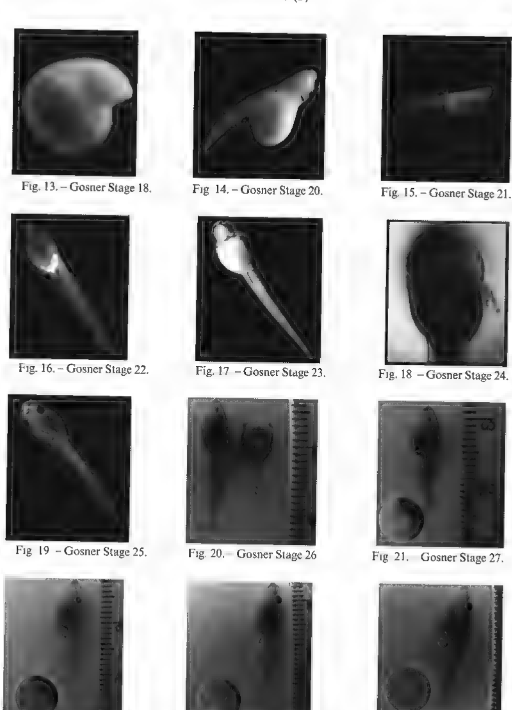


Fig. 13. – Gosner Stage 18.

Fig. 14. – Gosner Stage 20.

Fig. 15. – Gosner Stage 21.

Fig. 16. – Gosner Stage 22.

Fig. 17. – Gosner Stage 23.

Fig. 18. – Gosner Stage 24.

Fig. 19. – Gosner Stage 25.

Fig. 20. – Gosner Stage 26.

Fig. 21. – Gosner Stage 27.

Fig. 22. – Gosner Stage 28.

Fig. 23. – Gosner Stage 31.

Fig. 24. – Gosner Stage 32.

Fig. 13 to 24. – Developmental stages 18-32 (Gosner, 1960) of the tadpole of *Polypedates teraiensis*.

20. Gosner Stage 22 (fig. 16)

Age. – 140 h.

Total length. – 7.0–7.7 mm.

Characters. – The tadpole drops in water. The tail fins are transparent and blood circulation within them begins. The yolk reserve is quite large and elongated. Eyes distinct. Gills very well developed. Light pigmentation on the dorsal side but not around the eyes. Upper and lower labial fringes develop, but without papillae.

21. Gosner Stage 23 (fig. 17)

Age. – 162 h

Total length. – 8.2-10.4 mm.

Characters. Yolk still visible but reduced. Stomach region less bulging Developing operculum, with gills projecting below it. Papillae start developing on the upper and lower labial fringes. Darker pigmentation on dorsal side. Pigmentation extended up to the end part of the tail but gradually becoming lesser. No pigmentation around the eyes. Vent closed.

22. Gosner Stage 24 (fig. 18)

Age. – 179 h.

Total length. – 10.6–10.9 mm.

Characters. –Yolk still present. Gills reduced Operculum closed on the right side, gills on the left side distinct. Upper and lower jaw sheaths are developing. A faint row of upper keratodonts develops, the future uppermost row A1. Tail tip pointed. Dark pigmentation on the dorsal side, lighter on tail. Pigmentation on the ventral side just above the yolk plug and in the region of the mouth.

23. Gosner Stage 25 (fig. 19)

Age. – 197 h.

Total length. – 11.4–12.9 mm.

Characters. Gills disappeared, operculum closed. A faint line corresponding to the opening of the spiracle can be seen. Upper and lower jaw sheaths developed Serrations of the jaw sheaths not distinct. KRF 1:1+1/1+1.2. Digestive tract with three loops. Dorsal side darkly pigmented, lighter on the ventral side and on the end of the tail.

24. Gosner Stage 26 (fig. 20)

Age. – 312 h (13 days).

Total length. – 20.6–23.1 mm.

Length of hind-limb. – 0.17-0.23 mm.

Characters. Hind-limb bud visible, its length is half of its diameter Definitive KRF 1:3+3/1+1:2 reached. Pigmentation all over the dorsal side except around the eyes.

25. Gosner Stage 27 (fig. 21)

Age. 360 h (15 days).

Total length – 17.8–27.3 mm.

Length of hind-limb. – 0.32–0.47 mm

Characters. – The length of the hind-limb bud is equal to its diameter. Tail muscle well developed. Oral papillae well developed and slightly pigmented. Dark pigmentation on the dorsal side with a dark transversal band in the centre of the dorsal side.

26. Gosner Stage 28 (fig. 22)

Age. – 432 h (18 days).

Total length. – 20.6–23.1 mm.

Length of hind-limb. – 0.71–0.89 mm.

Characters. Limb bud elongated, equal or longer than its diameter, its distal end slightly conical. Keratodonts distinct. Pigmentation on the ventral side just above the intestinal coil.

27. Gosner Stage 29

Age. 456 h (19 days).

Total length. 20.6–28.8 mm.

Length of hind-limb. – 0.71–1.18 mm.

Characters. Length of limb equals to one and half times its diameter. Distal end of limb bud conical. Pigmentation on the ventral side extending near the mouth.

28. Gosner Stage 30

Age. – 468 h (19.5 days).

Total length. – 23.1–30.1 mm.

Length of hind-limb. – 0.7–1.90 mm.

Characters. Length of limb bud equals to twice its diameter. Distal half of conical limb bud bends slightly ventrally. Digestive tract with four loops.

29. Gosner Stage 31 (fig. 23)

Age. – 480 h (20 days).

Total length. – 28.4–31.7 mm.

Length of hind-limb. – 1.5–1.8 mm.

Characters. – Hind-limbs paddle shaped. Pigmentation lesser compared to the earlier stages but concentrated.

30. Gosner Stage 32 (fig. 24)

Age. – 642 h (26 days).

Total length. – 26.1–30.5 mm.

Length of hind-limb. – 1.5–1.8 mm.

Characters. The edge of the foot paddle becomes indented on the dorsal side, which marks the development of the 4th and 5th toes.

31. Gosner Stage 33

Age. – 672 h (28 days).

Total length. – 29.6– 33.0 mm.

Length of hind-limb. – 1.5–2.4 mm.

Characters. – The edge of the foot paddle becomes indented behind the prominence of 4th toe, which marks the 3rd, 4th and 5th toes. Pigmentation much lesser.

32. Gosner Stage 34 (fig. 25)

Age. – 720 h (30 days).

Total length. – 31.2 35.6 mm.

Length of hind-limb. – 1.5–3.9 mm.

Characters. – The edge of the foot paddle becomes indented, on the ventral side, behind the prominence of 3rd toe, which marks the prominence of 2nd, 3rd, 4th and 5th toes. Pigmentation darker than in the previous stage.

33. Gosner Stage 35 (fig. 26)

Age. – 768 h (32 days).

Total length. – 33.3–38.7 mm.

Length of hind-limb. – 1.8–3.9 mm.

Characters. The edge of the foot paddle is indented behind the 2nd toe, demarcating the prominence of the 1st toe. All the five toes are separated from each other. Digestive tract with five loops. Pigmentation negligible on the ventral side. Pigmentation uniform on the dorsal side with a distinct longitudinal dark line in the middle.

34. Gosner Stage 36

Age. – 864 h (35 days).

Total length. – 34.9–40.6 mm.

Length of hind-limb. – 2.12–5.0 mm.

Characters. – Margin of the 5th toe web directed towards the tip of the 2nd toe. Knee joint formed.

35. Gosner Stage 37 (fig. 27)

Age. – 936 h (39 days).

Total length. – 42.4–45.2 mm.

Length of hind-limb. – 7.4–9.9 mm.

Characters. – The margin of the 5th toe web is directed towards the tip of the 1st toe. Toe tips rounded. Webbing of feet distinct between 1st and 2nd toes as well as between 2nd and 3rd toes. Dark pigmentation on the dorsal side and on the tail region, fins pigmented.

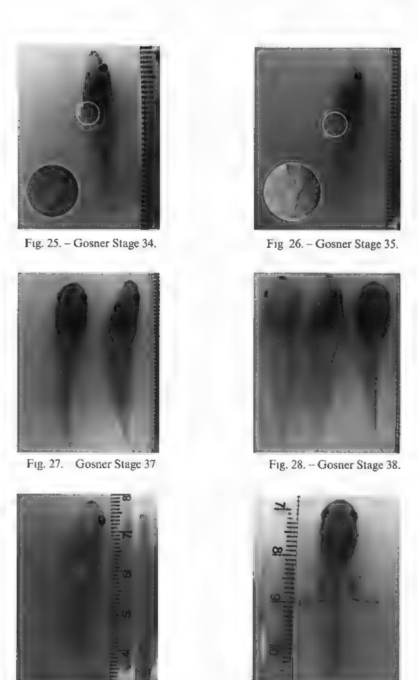


Fig. 25. – Gosner Stage 34.

Fig. 26. – Gosner Stage 35.

Fig. 27. – Gosner Stage 37.

Fig. 28. – Gosner Stage 38.

Fig. 29. – Gosner Stage 40.

Fig. 30. – Gosner Stage 41.

Fig. 25 to 30. – Developmental stages 34-41 (Gosner, 1960) of the tadpole of *Polypedates teraiensis*.

36 Gosner Stage 38 (fig. 28)

Age. – 1008 h (42 days).
Total length. – 39.3–45.5 mm.
Length of hind-limb. – 7.0–9.8 mm.
Characters. – The margin of the 5th toe web is directed towards the prehallux. The toe tips are rounded with slight pigmentation on the limbs. Pigmentation appears on the 3rd, 4th and 5th toes along the foot. Webbing of feet distinct between all toes. Foot-knee joint well developed. Appearance of metatarsal tubercle as a small outgrowth.

37. Gosner Stage 39

Age. – 1056 h (44 days).
Total length. – 43.0–45.6 mm.
Length of hind-limb. – 7.9–9.81 mm.
Characters. Subarticular tubercles appear on the inner surface of the toes as light patches. The inner metatarsal tubercle becomes a small oval outgrowth. Toe tips rounded with slight pigmentation. Developing forelimbs visible below the skin but not distinct. Digestive tract with six loops. Fins pigmented.

38. Gosner Stage 40 (fig. 29)

Age. – 1104 h (46 days).
Total length. – 42.6–50.0 mm.
Length of hind-limb. - 8.02 10.5 mm.
Characters. Toe tips are rounded. Subarticular tubercles are clearly elevated. Vent tube not yet reduced. All rows of keratodont present and distinct. Some of the keratodont rows are very faint due to loss of individual keratodonts. Muscles on the dorsal side are well built. Pigmentation lighter

39. Gosner Stage 41 (fig. 30)

Age. – 1128 h (47 days).
Total length. – 42.6–49.5 mm.
Length of hind-limb. - 10.8 15.2 mm
Characters. Vent tube reduced. Only a narrow strip remains over and in between bases of the thighs still attached with ventral fin distally. Skin over the forelimbs transparent. Tubercles on the hind-limbs distinct with pigmentation. KRF 1.2+2/1+1.2. All the keratodont rows faint due to shedding of individual keratodonts. Oral papillae remain intact. Digestive tract with five loops. Uniform pigmentation on the dorsal side.

40 Gosner Stage 42 (fig. 31)

Age. – 1176 h (49 days).
Total length. – 47.3–51.6 mm.
Length of hind-limb. 26.38–27.6 mm
Characters. The forelimbs emerge. Usually the right emerges first, followed by the left after a few hours, and the fingers have rounded tips. The webbing of the forelimbs is

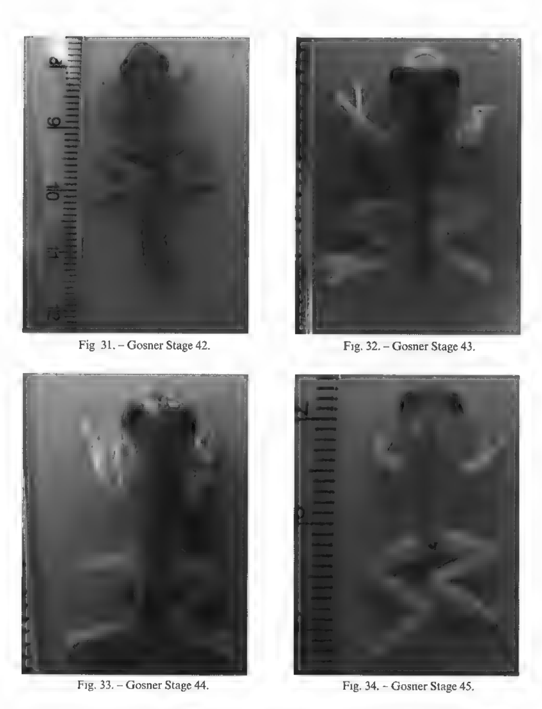


Fig. 31. – Gosner Stage 42.

Fig. 32. – Gosner Stage 43.

Fig. 33. – Gosner Stage 44.

Fig. 34. – Gosner Stage 45.

Fig. 31 to 34. – Developmental stages 42-45 (Gosner, 1960) of the tapdole of *Polypedates teraiensis*.

rudimentary, but as in the adult stage. The vent tube disappeared completely, leaving the vent aperture free below. The tail darkens and becomes shorter. Kerotodont rows and jaw sheaths are lost. Resorption of the labial fringe begins, however angular papillae still remain as a small tuft on both corners of the mouth, which starts widening The angle of the mouth is in level with the nostril.

41. Gosner Stage 43 (fig. 32)

Age. – 1224 h (51 days).
Total length. – 20.6–23.1 mm.
Length of hind-limb. – 18.8–26.8 mm.
Characters. Mouth opening widens. The angle of the mouth reaches a point midway between nostril and the anterior margin of eye. Eyes slightly protruding The dorsal and ventral fins disappear and the tail becomes shorter. Digestive tract with four loops. The pigmentation is uniform.

42. Gosner Stage 44 (fig. 33)

Age. – 1248 h (52 days).
Total length. – 17 6–18.6 mm.
Length of hind-limb. – 20.4–23.1 mm.
Characters. Eyes protruding. The widening angle of mouth reaches the level of the middle of eye. The dorsal and ventral fins completely disappeared. The tail becomes much shorter.

43. Gosner Stage 45 (fig. 34)

Age. – 1320 h (55 days).
Total length. – 14.9–15.8 mm.
Length of hind-limb. – 20.6–23.1 mm.
Characters. – The angle of the mouth reaches the posterior margin of the eye. The tail is reabsorbed to a small triangular stub which is dark in color.

44. Gosner Stage 46

Age. – 1392 h (58 days).
Total length. – 15.6–17.4 mm.
Characters. – The tail stub disappeared completely It is a metamorphosed froglet.

Conclusion

The total time for the completion of development was 58 days (1392 h). The most important developmental steps are summarized in table 1. Measurements of stages 22 46 are presented in tables 2-4.

Table 1. – Significant developmental stages of *Polypedates teraiensis*.

No.	Stage	Characteristics	Age
1	1	Fertilized egg	0 h
2	3	Two cell stage	2 h 25
3	10	Blastula	16 h
4	12	Gastrula	21 h
5	14	Appearance of neural fold	36 h
6	17	Appearance of tail bud	62 h
7	20	Hatching	104 h (4.3 days)
8	21	Distinct external gills	118 h (4.9 days)
9	25	Appearance of spiracle	197 h (8 days)
10	26	Appearance of hind-limb bud	312h (13 days)
11	35	Distinct five digits	768 h (32 days)
12	38	Appearance of metatarsal tubercle	1008 h (42 days)
13	42	Emergence of both forelimbs	1176 h (49 days)
14	46	Metamorphosed frog	1392 h (58 days)

Description of tadpoles at stage 38

External morphology   Stage 38 tadpoles (n = 10, collection numbers IASST.AT.1081 IASST.AT.1090; fig. 28) were studied in detail.

Tadpoles of moderate size (TL 39.3–45.5 mm; SVL 13.8–14.8 mm), generalized exotrophic tadpoles of Orton's (1953) type IV, lentic: benthic (Altig & Johnston, 1989).

In dorsal view body elliptical, widest at the middle of the intestinal coil, head oval with a blunt snout. In profile, body roughly ovoid Eyes of medium size (about 2 0 mm), bulging, positioned and directed almost laterally; interocular distance large (6.0 6.9 mm). Eyes placed closer to the spiracle (3 2 3 6 mm) than to the snout (4.3 4.8 mm). Pineal ocellus present, lying before the anterior edge of the eyes. Nares small, rimmed and closely spaced; internarial distance small (1.5–1.8 mm). Nares placed nearer to snout (1.6–1.9 mm) than to eyes (2.3–3.5 mm)

Spiracle sinistral, of moderate size (about 1 8 mm), rectangular shaped, flat, entirely attached to body wall, ventrolateral in position, closer to vent tube opening than to snout, oriented posterodorsally. Dorsal body musculature distinct. There are 5½ intestinal loops. Very short and dextral vent tube, ring-like, not attached to ventral fin, directed posterolaterally, opening dextral Glands absent. Lateral line system not observed, lacrymal canals present from stage 36 (at stage 35 a faint pigmentation is present along the canal, but the latter is not yet visible).



Fig. 35 – Picture of the oral disc of a stage 38 tadpole of *Polypedates teraiensis* stained with methylene blue (TL 44.2 mm, collection number IASST.AT 1088)

Tail length (25.9–31.8 mm) with delicate fins. Dorsal and ventral fins of nearly equal size, high (about 1/3 higher than maximum body height; MTH 7.8 9.7 mm), slightly convex, upper fin extending onto upper body (on a distance of about 1.9 mm). Tail tip greatly narrowing near tip, tip pointed.

Oral disc (fig. 35) of moderate size (ODW 2 8 2.9 mm), subterminal/anteroventral positioned and oriented anteroventrally, emarginated. One row of marginal papillae largely interrupted on the upper labium, and only very shortly in the centre of the lower labium. A row of submarginal papillae on the lower labium (also interrupted in the middle) and at the angle of the mouth Papillae rounded. Jaw sheaths serrated, upper jaw sheath a large arch with a weak median convexity, lower jaw sheath V-shaped. KRF 1 3+3/1+1 2. First row of the upper labium continuous whereas the 2nd, 3rd and 4th rows are interrupted. Innermost row of lower labium very slightly interrupted whereas the two other rows are continuous. This tadpole is overall herbivore. However zooplankton was also found during the gut content analysis, but as the number is very low it is considered as a chance entry.

Life coloration. The larvae are light brown with dark brown pigments. Ventral side light gray and transparent. A light point on the tip of the snout. Caudal muscle light brown, lighter that abdomen, fins transparent immaculate. In preservative, the colors fade and the ground color became beige, the ventral side creamy white.

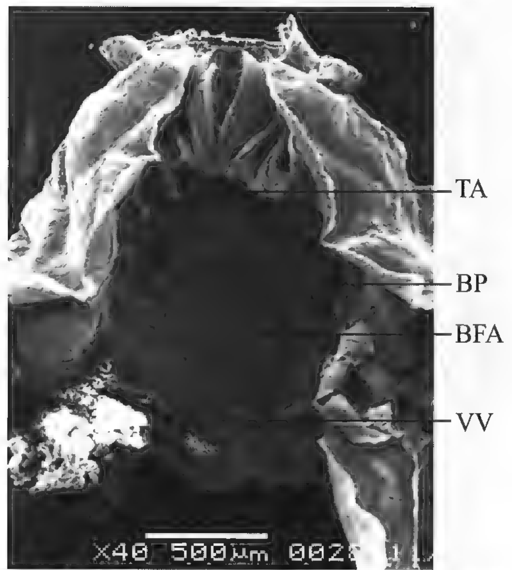


Fig 36 – Buccal floor of a stage 38 tadpole of *Polypedates teraiensis* (IASST.AT.1082). BFA, buccal floor arena, BP, buccal pocket; TA, tongue anlage; VV, ventral velum.

Buccopharyngeal anatomy – Buccal floor (fig. 36). Prelingual arena narrow with a pair of large infralabial papillae with their anterior edge pustulated. Tongue anlage rounded with two pairs of lingual papillae pustular on tip, the two median slightly longer than the lateral ones. Buccal floor arena wide, defined by about 9-10 moderately-sized papillae on each side; surface of floor arena with 20-25 pustules. Buccal pockets nearly oval, closer to the tongue anlage than to the ventral velum. Ventral velum continuous with spicular support and 10 projections, the median six closer together, medial notch present; secretory pits present on the velum. Branchial baskets exposed with three gill chambers on each side.

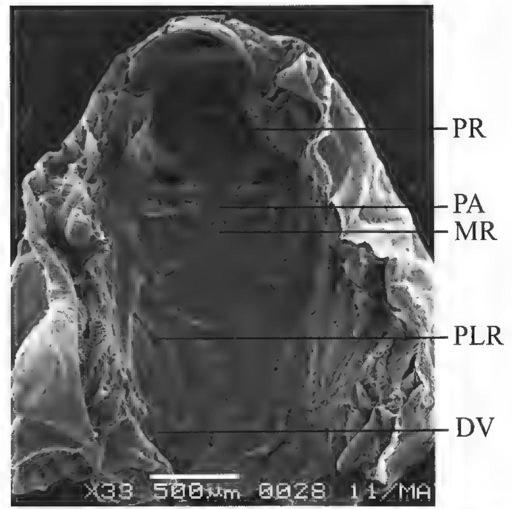


Fig 37. Buccal roof of a stage 38 tadpole of *Polypedates teraiensis* (IASST.AT.1082) DV, dorsal velum, MR, median ridge, PA, postnarial arena, PLR, posterolateral ridge; PR, prenarial arena

Buccal roof (fig. 37). – Prenarial arena slightly rectangular and concave with a semicircular pustular prenarial ridge. Prenarial papillae present, rising in the middle of the anterior narial wall; a few pustulations present on the anterior narial wall. Choanae slightly posteromedially oriented, almost oval. Narial valve smooth, elevated. Two pairs of transversely oriented postnarial papillae on the same transversal plane, the higher pair small and pustular at tip, the lowest pair long and pustular on most part. Median ridge low, with irregular small papillae on its free edge; at least two small papillae in the postnarial arena. Lateral ridge papillae triangular elongate, transversely oriented, bearing a few papillae on their anterior edge. Buccal roof arena defined by only three buccal roof arena papillae on each side, oriented slightly anteromedially, the medial one being the largest and having pustulated tip, the most anterior less pustular, the posteriormost smooth, buccal roof arena with about 35–40 small

Table 2. – Morphometric measurements of tadpoles of *Polypedates teraiensis* in stages 22 to 34. Mean ± standard deviation and range of 10 measured individuals per stage. See text for abbreviations.

	TL	SVL	SSp	TAL	MTH	HLL
Stage 22	7.5 ± 0.23 7.0–7.7	3.58 ± 0.111 3.45–3.86		4.16 ± 0.195 3.85–4.58	–	
Stage 23	9.1 ± 0.84 8.2–10.4	3.31 ± 0.197 2.90–3.60	–	5.5 ± 0.42 5.0–6.2	–	–
Stage 24	10.8 ± 0.105 10.6–10.9	3.65 ± 0.237 3.38–4.20	–	7.0 ± 0.13 6.9–7.2	–	–
Stage 25	12.2 ± 0.403 11.4–12.9	4.14 ± 0.140 3.88–4.28	–	7.9 ± 0.44 6.9–8.4	–	–
Stage 26	19.3 ± 0.781 20.6–23.1	7.0 ± 0.46 7.5–8.7	–	4.3 ± 0.49 4.5–4.8	–	0.19 ± 0.03 0.17–0.23
Stage 27	22.1 ± 3.68 17.8–27.3	8.3 ± 1.3 6.7–9.8	–	4.9 ± 0.68 3.9–5.9	–	0.40 ± 0.05 0.32–0.47
Stage 28	22.1 ± 0.986 20.6–23.1	8.0 ± 0.41 7.5–8.7	–	4.7 ± 0.14 4.5–4.8	–	0.78 ± 0.08 0.71–0.89
Stage 29	25.1 ± 3.32 20.6–28.8	9.1 ± 1.2 7.5–10.6	5.77 ± 0.454 5.20–6.18	17.0 ± 2.12 14.4–19.3	5.60 ± 1.06 4.48–6.62	0.99 ± 0.19 0.71–1.18
Stage 30	28.1 ± 1.94 23.1–30.1	10.5 ± 0.690 9.5–11.8	5.63 ± 0.359 5.20–6.23	18.5 ± 1.48 14.6–19.7	5.74 ± 0.126 5.56–5.98	1.11 ± 0.148 0.71–1.18
Stage 31	30.2 ± 0.970 28.4–31.7	11.0 ± 0.644 9.7–11.8	6.48 ± 0.168 6.14–6.78	19.9 ± 0.543 19.2–20.7	6.53 ± 0.214 5.94–6.68	1.68 ± 0.103 1.48–1.77
Stage 32	28.7 ± 1.56 26.1–30.5	10.4 ± 0.094 10.3–10.5	6.01 ± 0.174 5.80–6.22	18.9 ± 1.24 17.2–20.8	6.13 ± 0.213 5.84–6.39	1.68 ± 0.103 1.48–1.77
Stage 33	30.7 ± 1.30 29.6–33.0	10.7 ± 0.441 10.4–11.4	6.43 ± 0.530 5.98–7.30	20.4 ± 0.659 19.7–21.1	6.21 ± 0.211 5.96–6.49	1.77 ± 0.262 1.48–2.40
Stage 34	34.1 ± 1.39 31.2–35.6	11.9 ± 0.867 11.0–13.3	7.37 ± 0.364 6.42–7.80	22.6 ± 1.03 21.1–24.4	6.71 ± 0.379 6.48–7.40	2.21 ± 0.648 1.50–3.86

pustulations, more concentrated in the middle and fewer in the posterior region. Posterolateral ridge low and present laterally. Glandular zone present and continuous across the buccal roof, of about five secretory pits large, size of secretory pits decreasing anteroposteriorly. Dorsal velum pustular, interrupted medially.

Discussion

Northeastern India contains a rich assemblage of anuran species and is considered a biodiversity hotspot (Myers et al., 2000). Nevertheless, only a few studies on the annual breeding cycles of the amphibian in this region have been carried out. Some of them concern *Fejervarya "limnocharis"* and *Euphlyctis cyanophlyctis* from Shillong by Roy & Khare (1978) and Kumar (1982) respectively, *Humerana humeralis* (Boulenger, 1887) and *Hylarana lepto*

Table 3. Morphometric measurements of tadpoles of *Polypedates teraiensis* in stages 35 to 40. Mean ± standard deviation and range of 10 measured individuals per stage. See text for abbreviations.

	Stage 35	Stage 36	Stage 37	Stage 38	Stage 39	Stage 40
TL	35.9 ± 1.62 33.3–38.7	38.7 ± 1.67 34.9–40.6	43.8 ± 0.910 42.4–45.2	43.6 ± 2.06 39.3–45.5	44.9 ± 0.622 43.5–45.6	47.1 ± 2.20 42.6–50.0
SVL	12.7 ± 0.954 11.0–14.4	13.4 ± 0.789 12.3–14.5	14.9 ± 0.313 14.4–15.5	14.5 ± 0.292 13.8–14.8	14.7 ± 0.168 14.4–14.9	15.2 ± 0.993 13.6–16.7
BW	5.99 ± 0.526 5.20–6.90	7.04 ± 0.791 5.00–7.90	8.44 ± 0.248 8.20–9.01	8.54 ± 0.587 7.66–8.93	8.74 ± 0.385 8.20–9.45	8.87 ± 0.148 8.65–9.00
HL	6.31 ± 0.492 5.60–7.20	6.08 ± 0.788 4.80–7.20	6.43 ± 0.052 6.33–6.48	6.21 ± 0.619 5.01–6.84	6.40 ± 0.458 5.20–6.84	6.48 ± 0.141 6.30–6.74
IOD	6.00 ± 0.200 5.76–6.40	6.24 ± 0.658 5.08–6.90	6.57 ± 0.207 6.34–6.92	6.48 ± 0.260 6.02–6.94	6.49 ± 0.139 6.24–6.66	6.60 ± 0.165 6.42–7.00
NN	1.64 ± 0.140 1.50–1.90	1.63 ± 0.135 1.42–1.90	1.73 ± 0.036 1.68–1.80	1.73 ± 0.096 1.50–1.82	1.74 ± 0.034 1.68–1.78	1.75 ± 0.030 1.69–1.80
NPE	2.35 ± 0.102 2.20–2.50	2.57 ± 0.220 2.20–2.94	3.23 ± 0.034 3.18–3.26	3.00 ± 0.390 2.32–3.54	3.41 ± 0.191 2.09–3.55	3.46 ± 0.075 3.36–3.55
ODW	2.42 ± 0.145 2.23–2.60	2.65 ± 0.133 2.50–2.80	2.81 ± 0.026 2.78–2.86	2.84 ± 0.037 2.78–2.88	2.78 ± 0.105 2.66–2.88	2.87 ± 0.153 2.64–3.14
SSp	7.48 ± 0.209 7.18–7.80	7.63 ± 0.447 6.96–8.44	8.65 ± 0.063 8.58–8.79	8.57 ± 0.261 8.00–8.94	8.62 ± 0.143 8.40–8.86	8.73 ± 0.289 8.43–9.48
SN	1.32 ± 0.071 1.20–1.40	1.53 ± 0.206 1.24–1.82	1.82 ± 0.038 1.79–1.89	1.79 ± 0.101 1.60–1.89	1.76 ± 0.084 1.60–1.86	1.77 ± 0.058 1.62–1.81
SE	3.55 ± 0.142 3.31–3.72	3.98 ± 0.478 3.48–4.80	4.48 ± 0.133 4.32–4.64	4.57 ± 0.123 4.30–4.75	4.59 ± 0.087 4.50–4.75	4.65 ± 0.227 4.50–5.24
SpE	3.53 ± 0.167 3.30–3.80	3.29 ± 0.624 2.04–3.80	3.50 ± 0.042 3.40–3.54	3.49 ± 0.142 3.20–3.62	3.39 ± 0.299 2.74–3.62	3.61 ± 0.440 2.98–4.76
SpN	7.16 ± 0.257 6.80–7.50	7.22 ± 0.299 6.80–7.80	7.59 ± 0.055 7.44–7.64	7.51 ± 0.294 7.10–7.87	7.71 ± 0.139 7.46–7.87	7.79 ± 0.167 7.46–8.08
TAL	24.1 ± 1.15 22.2–26.3	25.9 ± 1.30 23.5–27.2	29.5 ± 0.609 28.5–30.2	29.9 ± 1.87 25.9–31.8	30.2 ± 1.95 25.9–31.9	31.9 ± 1.40 29.9–34.2
MTH	7.55 ± 0.775 6.48–8.66	7.78 ± 0.703 7.10–9.18	7.60 ± 0.245 7.12–7.82	9.14 ± 0.626 7.84–9.73	9.19 ± 0.463 8.30–9.92	9.13 ± 0.464 8.68–10.17
HLL	2.86 ± 0.641 1.82–3.86	3.38 ± 0.718 2.12–4.12	9.45 ± 0.421 8.69–9.96	8.75 ± 1.20 7.00–9.80	9.24 ± 0.776 7.90–9.81	9.22 ± 0.879 8.02–10.50

Table 4. - Morphometric measurements of tadpoles of *Polypedates teraiensis* in stages 41 to 45. Mean ± standard deviation and range of 10 measured individuals per stage. See text for abbreviations.

	Stage 41	Stage 42	Stage 43	Stage 44	Stage 45
TL	46.4 ± 2.65 42.6–49.5	49.6 ± [illegible] 47.3–51.6	22.3 ± 0.852 20.6–23.1	18.2 ± 0.362 17.6–18.6	15.1 ± 0.417 14.6–15.7
SVL	15.0 ± 1.02 13.6–15.8	18.6 ± 0.474 17.9–19.4	14.4 ± 0.821 12.7–15.2	15.0 ± 0.435 14.4–15.5	–
BW	8.63 ± 0.179 8.38–8.93	8.59 ± 0.273 7.88–8.81	5.70 ± 0.050 5.59–5.76	4.56 ± 0.070 4.50–4.69	6.11 ± 0.097 6.02–6.22
BH	7.64 ± 0.286 7.00–7.98	7.64 ± 0.392 7.38–7.98	4.25 ± 0.049 4.19–4.32	4.21 ± 0.022 4.18–4.23	6.56 ± 0.051 6.42–6.62
HL	6.56 ± 0.122 6.42–6.75	6.58 ± 0.207 6.10–6.77	5.68 ± 0.347 5.02–5.88	5.22 ± 0.153 5.10–5.60	5.35 ± 0.180 5.10–5.60
HH	5.98 ± 0.298 5.20–6.22	5.93 ± 0.345 5.20–6.22	5.58 ± 0.069 5.50–5.67	4.37 ± 0.172 4.06–4.58	6.20 ± 0.104 6.02–6.34
IOD	6.56 ± 0.145 6.42–6.90	6.54 ± 0.093 6.38–6.62	4.82 ± 0.050 4.75–4.88	5.13 ± 0.009 5.12–5.14	5.81 ± 0.036 5.78–5.85
NN	1.74 ± 0.036 1.69–1.80	1.78 ± 0.163 1.69–2.24	2.14 ± 0.051 2.10–2.20	2.67 ± 0.008 2.66–2.68	2.41 ± 0.086 2.32–2.48
ED	2.00 ± 0 2.00	2.65 ± 0.031 2.64–2.66	2.00 ± 0 2.00	2.00 ± 0 2.00	2.40 ± 0 2.40
NP	3.44 ± 0.135 3.10–3.55	3.43 ± 0.063 3.36–3.55	2.08 ± 0.018 2.06–2.12	1.46 ± 0.004 1.45–1.46	2.32 ± 0.031 2.30–2.40
ODW	4.62 ± 0.179 4.23–4.82	6.65 ± 0.008 6.64–6.66	7.05 ± 0.055 7.00–7.12	7.58 ± 0.013 7.56–7.59	6.63 ± 0.039 6.60–6.70
SN	1.80 ± 0.025 1.76–1.83	2.03 ± 0.015 2.02–2.06	1.59 ± 0.033 1.54–1.62	1.55 ± 0.013 1.54–1.58	1.75 ± 0.024 1.69–1.78
SE	4.51 ± 0.123 4.42–4.69	4.51 ± 0.138 4.15–4.69	3.27 ± 0.006 3.26–3.28	3.43 ± 0.052 3.36–3.47	2.74 ± 0.110 2.64–2.95
TAL	31.5 ± 1.57 29.3–33.6	31.0 ± 0.695 30.0–32.2	7.8 ± 0.21 7.6–8.2	3.5 ± 0.05 3.4–3.6	–
MTH	8.76 ± 0.710 6.86–9.44	8.72 ± 0.460 7.48–8.99	2.79 ± 0.116 2.64–2.96	2.87 ± 0.009 2.86–2.88	
HLL	9.23 ± 0.742 8.02–9.80	26.7 ± 0.415 26.3–27.6	20.8 ± 3.15 18.8–26.8	21.3 ± 1.08 20.3–23.1	22.3 ± 1.04 20.6–23.1
FLL	-	8.37 ± 0.105 8.20–8.52	7.11 ± 0.408 6.66–7.67	7.45 ± 0.095 7.20–7.51	7.60 ± 0.147 7.40–7.86

glossa (Cope, 1868) in Assam (BORTAMULI et al., 2010), and *Polypedates* "*leucomystax*" and *Hyla annectans* in Nagaland (KIYASETUO & KHARE, 1986 and AO & BORDOLOI, 2001, respectively). Furthermore Ao et al (2006) provided basic information for *Rana khare* (Kiyasetuo & Khare, 1986).

There are several reports on the development and metamorphosis as well as on the staging tables of Rhacophoridae species: *Polypedates* "*leucomystax*" (VILLADOLID & DEL ROSARIO, 1930; ALCALA, 1962; KIYASETUO & KHARE, 1986); *Polypedates maculatus* (MCCANN, 1932; MOHANTY-HEJMADI & DUTTA, 1988; GIRISH & SAIDAPUR, 1999; DUTTA et al., 2001); *Rhacophorus arboreus* (Okada & Kawano, 1924) (IWASAWA & KAWASAKI, 1979); *Rhacophorus malabaricus* (SEKAR, 1990); and *Rhacophorus pardalis* (ALCALA, 1962).

This paper describes the morphology and development of *P teraiensis*. It was found that *Polypedates teraiensis* completed its development and metamorphosis in 58 days and hatching took place after four days at an ambient temperature of 26–32°C. Most of the data on developmental time concerned *P* "*leucomystax*" from different locations throughout the range of this complex of species. KIYASETUO & KHARE (1986) studied development of *P.* "*leucomystax*" from Nagaland (although these individuals likely belonged to the *P. mutus*/*teraiensis* species group; DUBOIS, 1987; AO et al , 2003) The complete development took 57–58 days at room temperature of 15 (night) to 24°C (day). This developmental time was very close to our results despite the cooler temperature. The tadpoles allocated to *P. leucomystax* from Peninsular Malaysia hatched four days after laying at the stages 20–22 and began to metamorphose about seven weeks after hatching at air temperature of 24–34°C (YORKE, 1983). These data also agree with our results but, as the author did not refer to precise stages, comparisons are limited. SHERIDAN (2008) reported a larval life (post hatching) of 42 days and a size at metamorphosis of 19.4 mm for specimens of *P leucomystax* from Sakaerat (northeastern Thailand) Although the developmental time is still close to our results, the metamorphosed froglet of *P. leucomystax* is bigger than those in our study However, reared tadpoles are often smaller than wild ones (e.g., MOHANTY-HEJMADI & DUTTA, 1979). The complete development of *Polypedates leucomystax* from Negros Island (Philippines) took 70–100 days in laboratory rearing conditions at water temperature 24–30°C (ALCALA, 1962). The hatchling and exit of the nest occurred at stage 20, as in *P. teraiensis*, and the imagos reached a size of 16.2 20 2 mm. *Polypedates maculatus*, the common Indian tree frog, completes development and metamorphosis in 55 days, 30–35°C room temperature, at Bhubaneswar, Orissa (MOHANTY-HEJMADI & DUTTA, 1988). As in the latter species, tadpoles dropped from the nest 4–5 days after deposition and pigmentation appeared after tadpoles left the foam nest (MOHANTY-HEJMADI & DUTTA, 1988). Under natural conditions, embryos of *P maculatus* from South India completed embryonic development in nine days and hatched at stage 23; the total timing from day of oviposition to completed metamorphosis was 60 days. Species of the genus *Rhacophorus* (a close relative to *Polypedates*; e.g., GROSJEAN et al., 2008; LI et al., 2009; YU et al., 2009) also produce foam nests. *Rhacophorus malabaricus* completes metamorphosis in 68 days at room temperature 28–35°C (SEKAR, 1990), *R. arboreus* in 44 days at 22°C (IWASAWA & KAWASAKI, 1979) and *R. pardalis* in 60–100 days at water temperature of 24-30°C (ALCALA, 1962). Although these data are close to our results for *P. teraiensis*, the various species show interspecific variation To evaluate this variation, more data on intra-specific variation should be collected

Metamorphosis (i.e., stages 42–46, from emergence of forelimbs until completion of metamorphosis) lasts 9 days in *P. teraiensis*. This is longer than the few available data on the duration of metamorphosis in other species. DOWNIE et al. (2004) who studied timing of metamorphosis in 14 taxonomically and ecologically diverse species from Trinidad plus *Xenopus laevis* (Daudin, 1802) reported metamorphosis ranging from 2.0 to 7.3 days at room temperature of 25.0–28.5°C. Among the factors that could influence metamorphosis duration, these authors discussed three that could partially explain this long duration in *P. teraiensis* tadpoles: (1) relative large size of the prometamorphic tadpoles (more tissue has to be re-modeled); (2) low number of predators present in new-filled temporary water bodies (the *Polypedates* foam nests are sometimes built before depressions are filled by rain; GROSJEAN, pers. obs.); and (3) metamorphosing *Polypedates* are able to leave water in earlier stages of metamorphosis and climb and hide within vegetation, thus avoiding aquatic and most of terrestrial predators. However, these are potential explanations that need further testing because, as emphasized by DOWNIE et al. (2004), the natural history of froglets is well under-studied. Furthermore, few data are available in the Rhacophoridae to compare with our results: *P. maculatus* and *R. arboreus* undergo metamorphosis in five days (IWASAWA & KAWASAKI, 1979; MOHANTY-HEJMADI & DUTTA, 1988), whereas SEKAR (1990) reported a metamorphosis duration of 12 days in *R. malabaricus*. The metamorphosis of the Philippine populations of *P. leucomystax* is reported to last about two weeks (VILLADOLID & DEL ROSARIO, 1930), though these data are far from being precise.

The clutch size for *P. teraiensis* consists of about 100 eggs. This size is much less than that given in most of the published data for *P. maculatus* (210–719 eggs per clutch; MOHANTY-HEJMADI & DUTTA, 1988; GIRISH & SAIDAPUR, 1999) and *P.* "*leucomystax*" (100–900 eggs per clutch; VILLADOLID & DEL ROSARIO, 1930, YORKE, 1983; SHERIDAN, 2008). This low number could be due to reproduction in captivity and data from wild caught clutches must be obtained before considering this clutch size as characteristic of the species.

The eggs of *P. teraiensis* measure 2.0–2.2 mm in diameter. This is slightly larger than eggs of *P.* "*leucomystax*" from Sakaerat, northeastern Thailand (average 1.81 mm: SHERIDAN, 2008), *P.* "*leucomystax*" from Nagaland (1.73–1.75 mm: KIYASETUO & KHARE, 1986), and *P. leucomystax* from Philippine (1.7–2.0 mm: ALCALA, 1962; 1.0–1.5 mm: VILLADOLID & DEL ROSARIO, 1930). In *Polypedates maculatus*, eggs are also smaller than those of *P. teraiensis* (1.25–1.50 mm: MCCANN, 1932; MOHANTY-HEJMADI & DUTTA, 1988; DANIEL & SEKAR, 1989) and those of *P. megacephalus* (1.8–2.0 mm: LIU, 1950). On the contrary, eggs of species of the genus *Rhacophorus* are bigger than those of *P. teraiensis* (2.76 mm in *R. malabaricus*: SEKAR, 1990, 2.5 mm in *R. maximus* Günther, 1859: MCCANN, 1932; and 3.0 mm in *R. arboreus* and *R. pardalis*: ALCALA, 1962; IWASAWA & KAWASAKI, 1979).

Polypedates teraiensis breeds in rain-fed pools that are sporadically filled by rain and then dry at different speeds. In such an unpredictable habitat, desiccation is arguably the single most important environmental factor affecting larval survivorship, and species that breed in such ponds have evolved several traits that allow successful development. One of these traits is a high rate of larval development, as observed in this study. This rapid rate of development in *Polypedates teraiensis* may be advantageous, as it allows the larvae to metamorphose quickly and escape desiccation, but also reducing exposure to aquatic predators and diseases

as reported in other frog species (NEWMAN, 1988; DENVER et al., 1998; PARRIS & BAUD, 2004). The tadpoles of small temporary ponds have been reported to spend more time in feeding and develop faster than tadpoles from large permanent ponds, where the larvae spend more time hiding from predators and develop more slowly (PELTZER & LAJMANOVICH, 2004). Environmental factors also can regulate amphibian metamorphosis. Amphibian larvae respond to alterations in these factors through high level of plasticity in the developmental phenotypes (STEARNS, 1989, PFENNIG, 1990, 1992). Such plasticity may involve changes in the rate of developmental transition, adopting alternative morphologies and so on (NEWMAN, 1992; MCCOLLUM & VAN BUSKIRK, 1996).

The present study reports that foam nest is essential for the development of this rhacophorid species. When eggs were removed from the foam nest before hatching, the embryo did not develop further. In *P. maculatus*, tentatives of rearing just hatched tadpoles before they naturally go out of the foam nest also failed (MOHANTY-HEJMADI & DUTTA, 1988) indicating that a period of development inside the foam nest after hatching is necessary. It thus seems that such a minimum period of development in the nest is a pre-requisite for embryonic development in *Polypedates*. The foam nest has been suggested to protect the eggs and embryos from predators and desiccation (HEYER, 1969; DOWNIE, 1988, 1993). Also protection from thermal damage was suggested as white foam reflects heat (GORZULA, 1977).

The embryonic development takes place between stages 1 and 19. The first cleavage starts at stage 3 and divides the egg completely into two equal blastomeres. The formation of blastula takes 16 hours and occurs at stage 10. The next significant stage is the 12th when the gastrula is formed. The neural fold appears at stage 14 and the tail-bud appears at stage 17. The form of the tail as observed in the stages 18–20, i.e., first rolled up against the yolk then very fine and almost straight, is more similar to endotrophic tadpoles (e.g., in *Arthroleptis poecilonotus* Peters, 1863: LAMOTTE & PERRET, 1963; *Nimbaphrynoides occidentalis* (Angel, 1943): LAMOTTE & XAVIER, 1972; or *Nectophrynoides tornieri* (Roux, 1906): ORTON, 1949 than to exotrophic ones. The embryonic development continues up to stage 19 and finally the embryo hatches at stage 20 within the nest. The whole embryonic development takes place within the foam nest. The young tadpole in stage 21 stays within the nest and drops in water at stage 22.

The newly hatched larvae are very delicate, have a large yolk sac and external gills. At stage 21, the cornea becomes transparent but the tail fins are still opaque. The tail fins become quite transparent at stage 22 and blood circulation within them begins. The external gills slowly get reduced and finally are completely covered with the completion of the development of the operculum at stage 25. At this point a faint line corresponding of the spiracle opening can be seen.

The differentiation of the oral disc and keratodont rows begin at stage 23; by stage 25 the keratodont rows are quite distinct. On the upper labium there is one uninterrupted and one interrupted row of keratodonts whereas on the lower labium all three rows are already present, the third one being small in size. By stage 26, the larval KRF 1:3+3/1+1.2 is attained. This remains up to stage 39. Subsequently, the keratodonts start shedding and by stage 40 there are one uninterrupted row (but half the size of the original one) and two interrupted rows of keratodonts on the upper labium. On the lower labium three rows still remain but are very faint due to shedding of individual keratodonts. At stage 41, there is one interrupted row

on the upper labium and two uninterrupted rows on the lower labium, all very faint. With the emergence of the forelimbs at stage 42, the jaw sheaths and the keratodonts have completely disappeared. These results corroborate previous findings and are in agreement with developmental pathway of tadpoles with a KRF higher than 2/3 (GROSJEAN, 2006, and literature cited therein). The sequence of keratodont rows appearance is of a "proximal" type on each labium after the 2/3 formula is attained, a pattern common to the stream dweller tadpoles of Ranidae and Megophryidae (type E of ALTIG & JOHNSTON, 1989: fig. 5: 91). The marginal papillae of *P. teraiensis* appear at stage 23 that is earlier than usually in other species, whereas the formation of keratodonts and jaw sheaths is slightly delayed (THIBAUDEAU & ALTIG, 1988). The opening of the mouth widens gradually from stage 42, and by stage 44 the angle of the mouth reaches the level of the middle of the eye. Feeding activity generally stops after stage 42 and the larvae undergo fasting during the period of intestinal remodeling.

A very faint pigmentation is visible at stage 22 on the dorsal side and the larvae are fully pigmented by stage 38. In *P. maculatus*, the pigmentation is also reported to appear after the embryo escaped the foam nest at stage 22 (MOHANTY-HEJMADI & DUTTA, 1988). The toe web starts developing at stage 37, then is present between all toes at stage 38 as in the adult state. During the next stages, it develops conjointly with toes but its relative expanse does not change. During this time the toe tips also become rounded, the subarticular tubercles appear at stage 40 and gradually develop. At stage 41, the skin covering the forelimbs becomes transparent and they finally emerge at stage 42. The toes of the forelimbs have rudimentary web.

Many of the morphological variations of buccopharyngeal (buccal filters) and oral (papillae, keratodonts) features are correlated with the mode of feeding (e.g., carnivorous, suspension feeding, scraping; ALTIG & JOHNSTON, 1989; ORTON, 1953; WASSERSUG & HEYER, 1983). The oral apparatus of a typical exotrophic pond tadpole includes an oral disc composed of an upper labium with free lateral edges and two keratodont rows, a larger lower labium with free marginal edges and three keratodont rows, unmodified jaw sheaths, a wide dorsal gap in the marginal papillae and submarginal papillae laterally and ventrolaterally (CANNATELLA, 1999). The structures of the oral apparatus of *P. teraiensis* were found to be similar with this description except that the upper labium bears more than two keratodont rows. This species is generally herbivore but a few specimens of zooplankton were also observed during the gut content analysis (here considered as a chance entry).

The tadpoles of all *Polypedates* species have an ovoid body (i.e., BW/BH about 100 %), lateral eyes, and a flagellum at the tip of the tail. They are all globally very similar (for the species from Borneo, not discussed here except for *P. leucomystax*, see INGER, 1966, 1985). Comparison of the tadpole of *P. teraiensis* with other *Polypedates* tadpole species is extremely difficult, primarily because of the lack of accuracy in specific assignation of the described tadpoles (most of them assigned to *P. leucomystax*: FLOWER, 1896, 1899; SMITH, 1917; VAN KAMPEN, 1923; VILLADOLID & DEL ROSARIO, 1930; POPE, 1931; LIU, 1940, 1950; ALCALA & BROWN, 1956; INGER, 1956; ALCALA, 1962), and because of too succinct descriptions.

The descriptions of FLOWER (1896, 1899), SMITH (1917), INGER (1956), ALCALA & BROWN (1956) and ALCALA (1962) can be assigned to *Polypedates leucomystax* as these samples are from north Borneo (Sabah), Thailand, Malay Peninsula, Singapore, and Philippines. However, two different KRF are commonly found in Thailand, i.e., 1.4+4/1+1.2 and

Table 5 – Summary of two morphological characteristics among described tadpoles in the genus *Polypedates* including different populations of *P* "*leucomystax*". KRF, Keratodont Row Formula.

	KRF	Light point on the snout	References
P leucomystax (north Borneo)	1:(4+4)-(5+5)/1+1:2	Absent?	INGER, 1956
P. leucomystax (Philippines)	1:3+3/3 or 1:3+3/1+1:2	Present	ALCALA & BROWN, 1956, ALCALA, 1962
P leucomystax (Malay Peninsula, Singapore)	1:3+3/3	Present	FLOWER, 1896; SMITH, 1917
P leucomystax (mainland Thailand, Bangkok)	1:4+4/1+1:2	Present	FLOWER, 1899, SMITH, 1917
P maculatus (India)	1:3+3/3	Absent	MOHANTY-HEJMADI & DUTTA, 1988
P maculatus himalayensis (India, Nepal)	1:(3+3)-(4+4)/1+1:2 2:3+3:1+1:2	Absent	ANNANDALE, 1912; GROSJEAN, 2004
P megacephalus (China, Vietnam)	1:3+3/3 1:(3+3)-(4+4)/1+1:2	Present	POPE, 1931; LIU, 1940, 1950, CHOU & LIN, 1997, GROSJEAN, 2004
P mutus (Vietnam)	1:4+4/1+1:2	Present	GROSJEAN, 2004
P. teraiensis	1:3+3/1+1:2	Present	This study

1:3+3/3, the latter form being found only in Malay Peninsula The specimens of Bangkok show a light yellow point on the tip of the snout (FLOWER, 1899). The populations of the Philippines have a KRF 1:3+3/3 or 1:3+3/1+1:2 and bear a white dot on the tip of the snout (ALCALA & BROWN, 1956; ALCALA, 1962) wheras those of north Borneo have a KRF 1:(4+4)-(5+5)/1+1:2 (INGER, 1956) Substantial differences in KRF are observed among these geographical populations of *P. leucomystax*. Recent biogeographical and demographical investigation of these populations (BROWN et al., 2010) showed shallow genetic divergence among them although four clades were recognized. The first one comprised the northern Sunda Region (including Malay Peninsula, North Borneo and South Philippines), the second one comprised the southern Sunda Region, the third the North Philippines and the fourth Sulawesi. However the observed differences in KRF can also be due to ontological differences.

POPE (1931) recognized a form from Hainan (as *P l leucomystax*) and a form from mainland China (as *P. l megacephalus*) though clear differences are not evident (from his own statement). Furthermore, he found no differences between the two tadpole forms, we consider these samples to represent larvae of *P. megacephalus*. The KRF is 1:3+3/3. Tadpoles from West China (Sichuan) have a KRF 1:3+3/1+1:2, more rarely of 1:4+4/1+1:2 (LIU, 1940, 1950). Tadpoles collected from Sa Pa, Vietnam and described as *Polypedates* gr *leucomystax* in GROSJEAN (2004), here tentatively assigned to *P. megacephalus*, have a KRF 1:4+4/1+1:2. Finally, CHOU & LIN (1997) described the external morphology and the buccal features of tadpoles from Taiwan with a KRF 1:(3+3)-(4+4)/1+1:2 Though not noticed by POPE (1931),

a creamy (LIU, 1940, 1950), ivory (CHOU & LIN, 1997) or white (GROSJEAN, 2004) dot on the tip of the snout of the tadpole is present in this species.

The KRF of the tadpole of *P maculatus* is 1 3+3/3 (MOHANTY-HEJMADI & DUTTA, 1988) The subspecies *P maculatus himalayensis* shows two KRF 1:(3+3) (4+4)/1+1:2 (the most common) or 2:3+3/1+1:2 which is unique among known species (ANNANDALE, 1912, GROSJEAN, 2004). The size of this tadpole is greater than the others and it is brown colored (even after 40 years in preservative), whereas other species turn clear gray very rapidly.

Polypedates mutus has a KRF 1:4+4/1+1:2 and a clear dot on the snout (GROSJEAN, 2004). Its keratodont formula is distinct from that of *P. teraiensis*, thus corroborating the separation of the two species which are morphologically very close. So, although adults can be distinguished by the presence/absence of vocal sacs, the two species can also be distinguished with larval characters, emphasizing the importance of knowing larval stages, especially on the ground of integrative taxonomy

It is important to note that the contrast between the clear dot and the darker surrounding coloration fades in preservative and it could have escaped the attention of some describers.

A summary of these comparisons is provided in table 5.

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